

QUATERNARY CLOSED-CONE PINE FLORA FROM  
TRAVERTINE NEAR LITTLE SUR, CALIFORNIA

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Interest in the relation of plants to deposition of calcareous charged water as travertine, tufa or sinter has existed at least since the time of Vergil and Pliny. Most of the studies have been concerned with currently active springs, and discussion has tended to center around the role of bacteria and algae, primarily, in producing deposition or at least in increasing precipitation of calcium carbonate from calcium bicarbonate (Agardh, 1827; Cohn, 1862; Weed, 1888; Meunier, 1899; Jones, 1914; Kellerman and Smith, 1914; Emig, 1917; et al.). In some cases other plant structures such as leaves, twigs, wood, etc., have been noted. The Little Sur travertine terraces in Monterey County, California, are interesting not only in terms of their formation and related geologic history, but also because the plant fossils give additional evidence regarding the distribution of the closed-cone pine forest along the central coast of California during the Pleistocene.

The travertine outcrop was discovered by Durham during a class field trip in October, 1958, and collections were made at that time as well as during a similar trip the following year. Additional collections and reconnaissance studies were made by both authors later in the second year. Durham is responsible for the geologic observations and discussion herein. Thanks are due to Robert Simmonds for running the amino acid tests on the gastropod shells and to Allyn B. Smith for identifying the shells. Likewise appreciation is expressed to H. L. Mason for criticizing the manuscript and to Jack Wolfe for checking the determination of fossils as well as for criticism of the manuscript. Most of the plant fossil specimens are located in the Paleobotanical Collections of the Department of Botany, University of Illinois. Duplicate specimens are deposited in The Museum of Paleontology, University of California at Berkeley. Voucher specimens for description of the modern vegetation are in the Herbarium of the Department of Botany, University of Illinois.

## FORMATION OF TRAVERTINE

The term "travertine" has been used for the Little Sur deposits because it seems to be the most inclusive term for deposits of this type. Emig (1917) has pointed out that the use of terms associated with this type of deposit has been varied and confused. He uses the term "travertine" for deposits of white, gray or brown concretionary calcium carbonate with cavernous and irregularly banded structure, soft and chalk-like to hard and crystalline, often containing leaves, twigs and mosses. Emig likewise indicates that "tufa" is a "more ancient term" for travertine which was used by Vergil and Pliny in the same sense that travertine is now used in

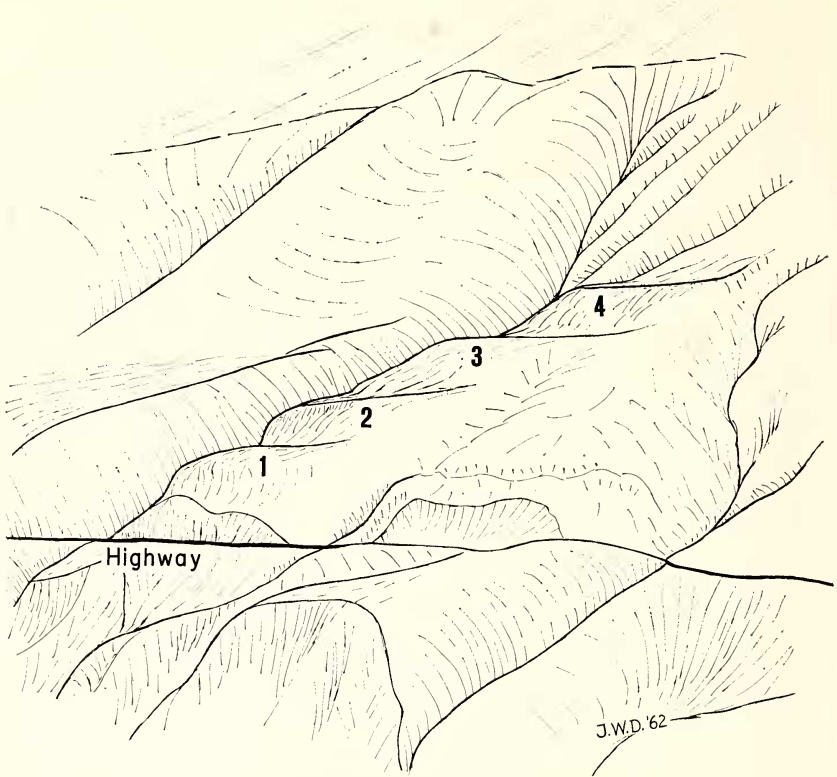


FIG. 1. Sketch of travertine terraces as seen from south. California State Highway 1 in foreground.

Italy. He considers tufa as a cellular variety of calcite that has been deposited from calcareous springs around nuclei of algae, mosses, leaves, twigs and other plant structures. Another term which has indiscriminately been interchanged with travertine by some is "calcareous sinter" (Weed, 1888). In its original German sense sinter means dross from iron and implies an initial process of heating before deposition takes place. Thus Emig thinks that deposits formed in the immediate vicinity of hot springs may be correctly called "sinter." Twenhofel (1950) indicates that calcareous deposits around springs are known as travertine, but distinguishes tufa and sinter as porous and travertine as compact and banded.

The material from the Little Sur occurrence varies from a very soft chalky, cavernous rock to hard, finely crystalline concretions and bands. It varies in color from white to creamy to ochreous, and at times is stained with ferrous iron. Because of the proximity of the Serra Hill fault (Trask, 1926), it seems probable that the terraces were produced as a result of hot springs activity along this fault. Hot springs are also known to occur at the present time about twenty-one miles south of the area

along the Sur Thrust. Preservation of the leaves is often relatively poor, probably because of the effect of their having fallen into a hot spring, as well as the manner in which the calcium carbonate was precipitated. Furthermore, it is difficult to uncover the fossils in their entirety because they do not occur along a bedding plane and because frequently the margins of the leaves are curled under.

#### LITTLE SUR TRAVERTINE TERRACES

The terraces are located in the Santa Lucia Mountains, Monterey County, California. They are exposed along State Highway 1, nearly one mile north of the mouth of Little Sur River (lat.  $36^{\circ} 20.7' N.$ , long.  $121^{\circ} 53.45' W.$ ).

There are four prominent terraces on the east side of the road and on the south side of a prominent ravine (fig. 1), and there is seemingly at least one below the road on the cliffs extending to the ocean. There is considerable marble (Sur Series) cropping out of the hill slopes to the east of the presumed location of the Serra Hill Thrust fault (Trask, 1926) and also on the north side of the ravine. According to Trask's map, the bedrock underlying the terrace deposits should be sediments of the Cretaceous "Chico Group." The south side of the present ravine on the north edge of the terraces has been cut into travertine which is 40–50 feet thick in places. It seems probable that the hot springs forming these deposits were in an old swale associated with the Serra Hill fault, and were located on an old surface prior to the development of the details of the present topography; the cascading pools were responsible for the sequence of terraces now observed. For convenience, the terraces have been numbered in sequence from the highway up the slope to the highest recognized, with the forefront of Terrace 1 being exposed in part in the road cuts. The apparent terrace below the road was observed from a distance only and is not included in the following descriptions.

Terrace 1 extends approximately 120 feet from north to south; Terrace 3, which is smaller, extends 200 feet from north to south; Terrace 2 is a little over 150 feet in the same direction as is Terrace 1. The frontal deposits of Terraces 1 and 2 are each at least 40–50 feet thick.

The thickest accumulation of travertine is near the south margin of the adjacent ravine, seemingly indicating that the center of accumulation was either at that point or near the axis of the present ravine. The deposits thin to the south, but Terraces 3 and 4 extend from the ravine on the north to the gully to the south where their southern extent is truncated by the present topography. Terraces 1 and 2 do not extend that far south.

The lower part of the deposit consists of occasional pure layers and tongues of travertine intercalated with alluvial gravels. In the roadcut exposures and outcrops at the north end of Terrace 1, the upper 15–20 feet of sediments are much purer travertine than the lower part. The lower part of this interval has beds with concentrated masses of *Cupressus*

branchlets as well as a few pine cones. Just below the *Cupressus* band there is a zone with abundant leaves of plants such as *Ceanothus*, *Garrya*, *Rubus*, *Ribes*, etc. Occasional masses of abundant *Equisetum* or leaves of the above plants are scattered in the exposures along the roadcut.

Much of the surface of the undisturbed exposures above the highway is covered with a dense caliche that probably conceals the fossil content. The best fossil collecting was in the roadcut and in the exposures at the north end of Terrace 1 on the south side of the ravine. On the upper terraces the most abundant fossils observed were sedge-like leaves with scattered *Garrya* leaves. On the forefront of Terrace 2 clumps of sedges were noted in growth position, apparently indicating water flowing downhill through a series of small pools.

The time of formation of the travertine terraces can not be determined directly at the present time. Trask (1926) considered the faulting in the area to have occurred at the end of the Pliocene, but this might indicate mid-Pleistocene in present-day terms. Topographically, the terraces appear to be situated on the upper part of the "steeply inclined slopes below" of Trask (1926, p. 176). However, the present sea cliffs in this area are obviously being eroded into this older topography and both the north and south edges of the terraces have been truncated by the erosion producing the present topography. Thus the terraces must be younger than Trask's "steeply inclined slopes below," and older than the present cycle of erosion. The ravine on the north is more than 50 feet deep where it cuts through the terraces and probably required considerable time for its formation.

Two gastropods which occur commonly in the travertine were identified as *Plespericola pinicola* Berry and *Helminthoglypta dupetithouarsi* (Deshayes) by Allyn G. Smith of the California Academy of Sciences who stated that he can not distinguish the fossil specimens from those living in the area today; consequently he would think that the terraces were Sub-Recent in age. However, Mr. Robert T. Simmonds (unpublished Ph.D. thesis, Univ. of Illinois) has been studying gastropods of the general *Polygyra* group from the Recent and the Pleistocene to see if it is possible to establish ages by means of amino acid deterioration in the shells. Mr. Simmonds ran chromatogram tests for amino acids on the shells of fossil specimens of *Helminthoglypta dupetithouarsi* from the travertine and on present-day specimens from the terraces. On the basis of his amino acid dating technique, Simmonds states that the fossil shells in the travertine definitely predate historic times and in all probability are more than 10,000 years old. A possible uncertainty in accepting the amino acid date might be the effect of heat (from the warm water of the hot springs) on deterioration of the amino acids. It is thought, however, that by the time the water had reached the surface and the travertine had been precipitated, the temperature must have been lowered to a point where it would not seriously affect the amino acids. The age of 10,000 or more years would appear to be substantiated by the in-

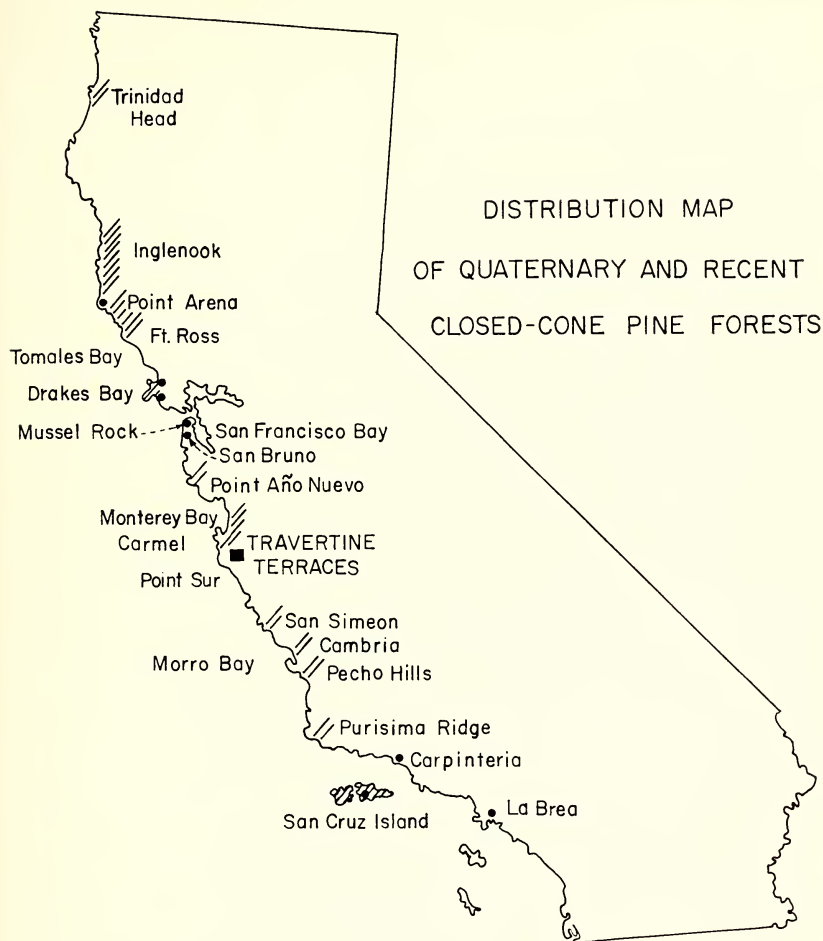


FIG. 2. Map showing distribution of Pleistocene and recent closed-cone pine forests in California. Slanted lines indicate present-day distribution and black circles indicate fossil records of closed-cone pine forests.

ferences from the topographic relationships of the terrace deposits.

The plant fossils do not furnish conclusive evidence as to the age of the deposits as during the Pleistocene the coastal region of California did not have changes in flora comparable to those elsewhere apparent during the change from glacial to interglacial epochs. Mason (1934) indicates that northern plants range farther south but the general aspect of the flora was the same. A lag in plant response to climatic fluctuations has made the presence of northern species useless as a means of detailed correlation at the present time. It is only at the periphery of the distribution of the flora that differences can be noted which may be used for this purpose.

## FOSSIL PLANTS FROM THE TRAVERTINE

Most of the fossils preserved in the travertine are impressions of leaves, with a few casts of stems and cones. In most of the other Pleistocene deposits recording the history of the closed-cone pines in California, i.e. Carpinteria, Santa Cruz Island and Tomales Bay, there have been many more fruits or seeds preserved than leaves. Several samples of the travertine were tested for pollen and spores, but no recognizable remains were observed.

Of the species represented by the travertine fossils, the following are considered to be forest plants: *Pinus radiata*, *P. muricata* (?), *Pseudotsuga menziesii* (?), *Cupressus* cf. *goveniana*, *Quercus agrifolia*, *Myrica californica*, *Ribes* cf. *sanguineum* var. *glutinosum*, *Rubus* cf. *parviflorus* (?), *R.* cf. *vitifolius* (?), *Ceanothus* cf. *griseus*, *Garrya elliptica*; and the following hydric or streamside plants: *Equisetum* cf. *hiemale* var. *californicum*, *Carex* spp., *Juncus* spp., algae.

Descriptions of the fossils and discussions of the modern occurrence of the species represented follow.

*PINUS RADIATA* Don and *P. MURICATA* Don (fig. 3, *g* and *h*). Casts of three partially preserved cones were found in the lower beds of Terrace 1. Preservation is poor, or at least the cones appear to have been weathered previous to being incorporated into the travertine. One specimen has only the lowermost scales preserved; however, the umbos are rounded to a knob which is a distinctive character of *P. radiata*. Another specimen has what appears to be one side of the cone preserved. It is 8 cm. long and ca. 5 cm. wide. The umbos on the lower scales are rounded, but they are also of a form which might be interpreted as that of *P. muricata*. The third specimen is so poorly preserved that it can only be stated that there is indication of a pine cone. However, below the piece of cone there appears to be a fascicle of three needles. *Pinus muricata* has two needles in a fascicle whereas *P. radiata* may have either three or two needles. The needles appear to be narrower than the average for extant *P. radiata*. As a result of some operation that caused the margins of the needles to become inrolled toward the midvein, the needles are circular in cross section and their width has been reduced. This inrolling may have occurred if they dropped into hot spring water. There also appear to be other scattered fragments of needles which may be turned on edge.

Fossil cones and wood of *P. radiata* have been found in the Pliocene Merced Sandstone (Glen, 1959), the Pleistocene deposits at Mussel Rock, at Carpinteria, and at Tomales Bay. *Pinus radiata* is the most abundant species in the Tomales deposit where it is represented by wood, cones, and leaves. The only previously known fossil occurrence for *P. muricata* is the Tomales Formation where it was far less abundant than *P. radiata*.

At present *P. radiata* is a coastal endemic of central western California, occurring from Pescadero, San Mateo County south to San Simeon, Monterey County. A variety also occurs on the coastal islands off of southern

California. *Pinus muricata* ranges discontinuously through about ten degrees of latitude, from Trinidad Head in Humboldt County to La Purísima Ridge in Santa Barbara County, thence southward through insular California to Guadalupe Island. On Huckleberry Hill near Monterey both *P. radiata* and *P. muricata* occur together but *P. muricata* tends to occur on shallow soils.

*PSEUDOTSUGA MENZIESII* (Mirb.) Franco(?). Another cast which is apparently a cone has a maximum length of 2.5 cm. and diameter of ca. 2 cm. It suggests either *Picea* or *Pseudotsuga*. There is no indication of the bract subtending the cone scale which is the usual means of identifying living *Pseudotsuga menziesii*. This has been true of all of the other Pleistocene records of the species (Mason, 1927, 1940; Potbury, 1932; Chaney and Mason, 1934); however, in Carpinteria and Tomales deposits, the portion of the bract lying underneath the cone scale and protected thereby, is preserved. This serves as a means of separating fossil cones of *Pseudotsuga* from those of *Picea*. In the Tomales flora certain fossils were identified as *Picea* because the cones bore a greater number of scales in proportion to their size than do those of *Pseudotsuga* and also because needles and twigs were found. Preservation of the Little Sur material is too poor to make positive determination possible. Mason (1934) states, however, that Tomales is the southern limit of the known range of *Picea* in the Pleistocene.

*Pseudotsuga* perhaps shared dominance with *Pinus radiata* and *P. muricata* of the forests about Tomales Bay in the Pleistocene as indicated by the hundreds of parts of cones. *Pseudotsuga* has also been reported from the Willow Creek flora on Santa Cruz Island. It has been recorded in the Pliocene of California (Dorf, 1930) where it is most often associated with *Sequoia*.

The modern range of *Pseudotsuga menziesii* along the coast is from Salmon Creek in the Santa Lucia Mountains northward to the northern end of Vancouver Island, British Columbia.

*CUPRESSUS* cf. *GOVENIANA* Gord. (fig. 3, b). Concentrated masses of branchlets of *Cupressus* occur in the lower part of Terrace 1, in the same interval where the pine cones were found. The branchlets are ca. 1–1.5 mm. wide; the leaves likewise are approximately 1–1.5 mm. long, opposite, appressed, acute but tending to be more or less blunt. Two cupressoid fructifications were found.

Species of *Cupressus* are common in the California Pleistocene, being reported from La Brea, Carpinteria, Santa Cruz Island and Tomales deposits. Mason (1927, 1934), however, points out the difficulty in specific identification of fossil material because of the close relationships among the various modern species. Determinations must be based largely upon ecological considerations suggested by the association of species and in many cases such a determination can not be accepted as final.

*Cupressus macrocarpa* is restricted to granodiorites on the headlands of Monterey Bay where it is an associate of *Pinus radiata*. *Cupressus goveniana* occurs around Monterey on the Monterey Shales, and is associated in the highlands with both *Pinus radiata* and *P. muricata*. In Mendocino County *Cupressus pygmaea* occurs in the vicinity of Fort Bragg, where it is an associate with *Pinus muricata*, *Pseudotsuga menziesii*, *Picea sitchensis*, *Tsuga heterophylla* and *Sequoia sempervirens*. The only other possibility for these fossils is *Cupressus sargentii* which has the widest range of the species of *Cupressus* in California. It is not strictly coastal although it is reported from some localities near the sea. It ranges from the southern Santa Lucia Mountains north to Mendocino County. Despite its wider geographic distribution, it tends to be limited to serpentine outcrops. Thus from the location, general association and the absence of granodiorites in the vicinity of the terraces, it appears that the branchlets in the travertine are more likely to be referable to *C. goveniana* than the other species.

*QUERCUS AGRIFOLIA* Nee (fig. 3, e; fig. 4, e). Upon initial study, the abundant specimens of *Garrya elliptica* were thought to be variable forms of *Quercus agrifolia*. However, close investigation of the venation patterns showed that a few specimens only were probably *Quercus*. These specimens occurred in the same beds with those assigned to *Garrya*. No fructifications were found.

*Quercus agrifolia* has been reported in the Pleistocene both from the asphalt beds of Rancho La Brea (Frost, 1927) and Carpinteria as well as the Tomales Formation (Mason, 1934). The Carpinteria material is more nearly like the shrub form of the species, i.e. those occurring on sterile shoots or crown sprouts that come up after fire. Neither acorns nor cups were found in the Carpinteria deposits, although they are common at Tomales Bay and elsewhere in the Pleistocene.

The modern *Q. agrifolia* typically is a coastal oak ranging through the coastal mountains of central and southern California. In the isolated remnants of the original closed cone-pine forests scattered from La Purisima Ridge northward to Sonoma County coast, *Q. agrifolia* is the dominant

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EXPLANATION OF FIGURE 3.

FIG. 3. Fossils from Little Sur travertine deposits. *a*, *Rubus* cf. *parviflorus* Nutt. Portion of folded leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-1. *b*, *Cupressus* cf. *goveniana* Cord. Branchlet and possible fructification.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-3. *c*, *Rubus* cf. *parviflorus* Nutt. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-2. *d*, *Ribes* cf. *sanguineum* var. *glutinosum* (Benth.) Loud. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-4. *e*, *Quercus agrifolia* Nee. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-6. *f*, *Ribes* cf. *sanguineum* var. *glutinosum* (Benth.) Loud. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-5. *g*, *Pinus muricata* Don? Portion of cone.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-7. *h*, *Pinus radiata* Don. Portion of cone.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-8.



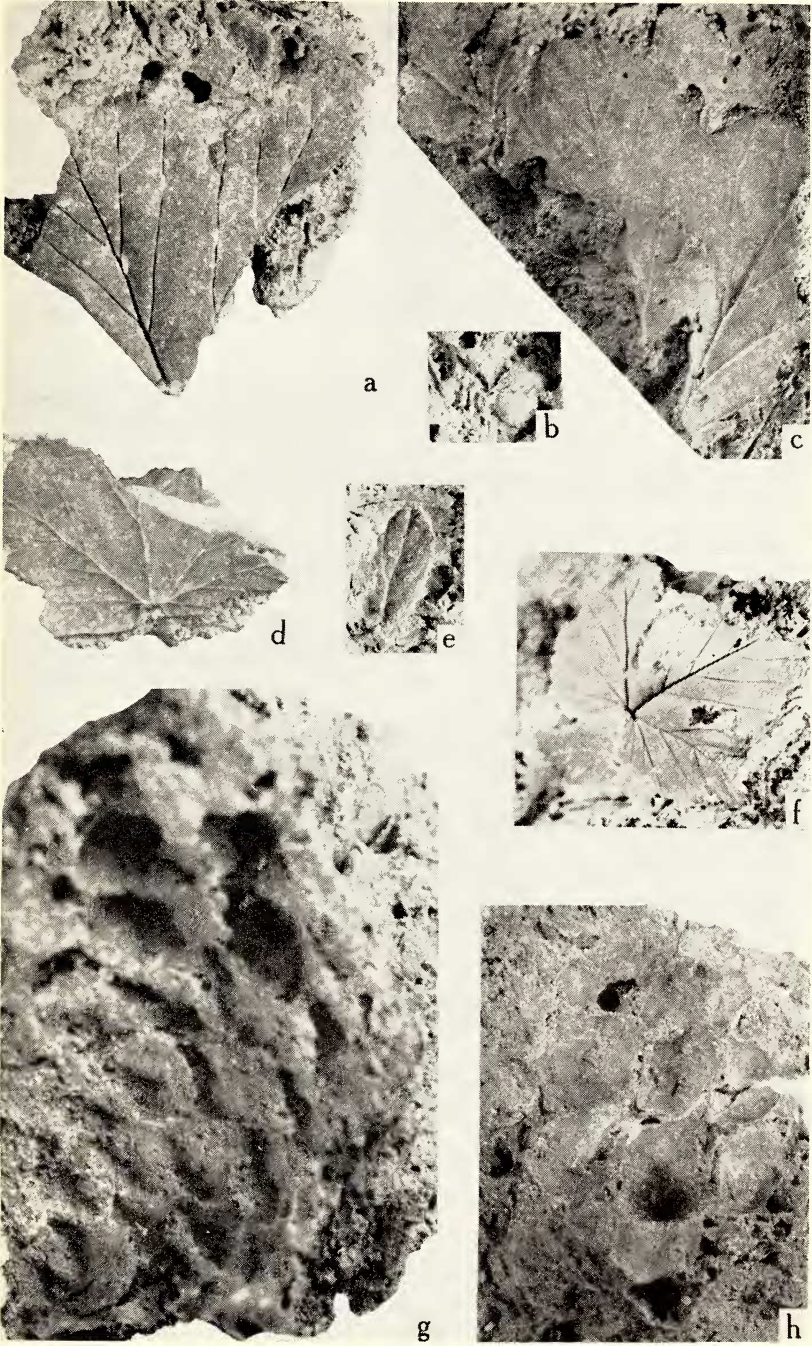


FIG. 3. Fossils from Little Sur travertine deposits.

understory tree in the forest. From the basis of general association, it seems probable that these fossil leaves are referable to *Q. agrifolia*.

*MYRICA CALIFORNICA* C. & S. A single leaf impression is suggestive of *Myrica californica*. It is ca. 4 cm. long and 1 cm. wide, and the dentition is not preserved because of strong inrolling of the margin of the leaf. Although preservation is not sufficient for unquestioned identification, the venation seems to indicate this species.

*Myrica californica* is represented in the Pleistocene deposits of Tomales Bay by an abundance of fruits and a few leaf impressions from indurated nodules. It is also known from the Santa Cruz Island and Carpinteria floras. No records are available from the more arid Rancho La Brea deposits.

The extant *Myrica californica* is strictly a coastal plant, attaining its best development only on the coastal side of the mountains in valleys immediately exposed to the sea. It ranges from the Puget Sound region southward through the coastal area of Oregon and northern California, thence becoming rarer southward where it extends to the Santa Monica Mountains of southern California. Mason (1934) suggests that the southernmost records of present distribution are probably relicts of Pleistocene distribution. The distribution of *Myrica californica* ends abruptly in the region of what probably was the southernmost extension of the cool humid Pleistocene climate.

*RIBES* cf. *SANGINEUM* var. *GLUTINOSUM* (Benth.) Loud. (fig. 3, d and f). *Ribes* leaves occur frequently with *Rubus* in beds of Terrace 1. As in the case of the other leaves, none are preserved in entirety, with masses of fragments occurring on top of each other. Almost all of the fragments are bent and frequently the edges turned under. The leaves are rounded in general outline with palmate divergence of three major veins indicating three lobes. They average 2–5 cm. wide. These characters tend to indicate the *Ribes sanguineum* group, although the venation pattern fits the variety *glutinosum* better than the typical form. The variety now occurs in open places or brushy sites or in the closed-cone pine forest from Santa Barbara to Humboldt County. There is no previous Pleistocene record.

*RUBUS* cf. *PARVIFLORUS* Nutt. and *RUBUS* cf. *VITIFOLIUS* C. & S. (fig. 3, a and c). In the lower beds of Terrace 1 *Rubus* leaves occur commonly. They tend to be found with masses of *Ribes* leaves and usually apart from the large concentrations of *Ceanothus* and *Garrya* which occur in the same sequence of beds. As usual only fragments of the leaflets are preserved, with the specimens being bent and folded so that it is difficult to determine the nature of the whole leaflet in most specimens. Some of the specimens are generally ovate in shape with others being palmately lobed. The size likewise varies greatly with the amount of the fragment preserved. Venation characters help indicate the size, however, especially by indicating the possibility of lobing. In many fragments the venation is

pinnate toward the terminal portion of the leaflet, but where the lower portion of the leaflet is preserved there is palmate divergence even though the lobe may not be intact.

The characters of some of the fragments suggest *Rubus vitifolius* as leaflets of this form may be either ovate or palmately lobed. However, other specimens, in terms of larger size and nature of the lobing appear to fit *Rubus parviflorus* better. Thus there appears to be little question of the presence of *Rubus*, but the amount of a leaflet preserved raises a question as to specific determination.

The only known Pleistocene record of *Rubus vitifolius* is from Tomales Bay (Mason, 1934) although Mason assumed that it was present in most of the coastal region of California. At present *Rubus vitifolius* is one of the most abundant shrubs in the valley and low hill country of California, occurring chiefly along streams and springy flats.

*Rubus parviflorus* fruitlets occur in the Pleistocene beds of Tomales Bay and from the San Bruno deposits. At the present time it is common along canyon streams and in open woods from southern California to Alaska. A clearly marked variety, called *velutinus*, occurs at the present time in the closed-cone pine and redwood forests near the coast from Santa Barbara to Mendocino County. It frequents streambanks and moist swales not too exposed to the sun.

CEANOTHUS cf. GRISEUS (Trel.) McMinn (fig. 4, b and c). *Ceanothus* leaves are abundantly represented in Terrace 1 in the beds which likewise frequently contain *Garrya* and sedge-like leaves. The leaves appear to have fallen in great quantities into the pool at one period, as the specimens are frequently laid one on top of the other. The specimens are fragmentary with the edges of the leaves universally curled under. This is due not only to the possible curling effect of hot water, but also to the natural tendency of leaves of some species of *Ceanothus* to be revolute. Because the edges are curled, it is impossible to determine the margin. The shape generally is oblong-ovate to broadly elliptical. The portion preserved varies in length up to 4 cm., indicating that some were even longer. The greatest width is 2.5 cm. with 1.5 cm. being common. Some show three prominent veins, although a few have only one. The lateral "reticulate" venation pattern is also prominent. These characters fit within the range described for *C. thyrsoflorus* or *C. griseus*. At one time *C. griseus* was considered a local variant of *C. thyrsoflorus* (Jepson, 1925), although recently it has been raised to specific status (McMinn, 1942; Munz and Keck, 1958).

*Ceanothus thyrsoflorus* is native to the cool coastal region from Santa Barbara County, California, north to Douglas County, Oregon, being especially abundant in the redwood belt of central and northern California. On the Monterey Peninsula it is replaced by *C. griseus* which occurs with the closed-cone pines and on the open slopes in the chaparral. Both of these species hybridize with other species of *Ceanothus*, providing ad-

ditional sources of variation. The general characters preserved in these fossils place them within either the group of *C. thyrsiflorus* or that of *C. griseus*. The habitat and the associated community however suggest *C. griseus*.

*Ceanothus thyrsiflorus* has been reported from the California Pleistocene beds of Santa Cruz Island, Carpinteria, San Bruno and Tomales Bay. Mason (1934) states that the one leaf impression from the Tomales flora looks much like the *griseus* variant, but restricts his identification to *C. thyrsiflorus*.

GARRYA ELLIPTICA Dougl. (fig. 4, d and f). Fragments of leaves that appear to be *Garrya* occur most abundantly in beds of Terrace 1, just below the zone containing the masses of *Cupressus* branchlets. However, they occur occasionally in deposits of the upper terraces where sedge-like leaves are the predominant observed fossils. The fact that only *Garrya* was found with the sedges, however, may be more a function of the exposures being covered with caliche and thus either masking the other fossils or rendering access to fossils very difficult in the upper terraces. On the other hand, the leaves of *Garrya* are more coriaceous than most of the others found and thus may have been preserved better under the possibly more unfavorable conditions in the upper hot pools.

The portions of the leaves preserved vary from 3 to 6 cm. in length and they indicate that the entire leaves must have been oblong or elliptic. Few leaf margins are intact, the edges usually being curved under. The general character of the leaf is within the range of variability occurring in *Garrya elliptica*, although one could easily confuse leaves of this group with those of the live oaks (particularly *Quercus agrifolia*).

*Garrya elliptica* is a coastal species ranging through west-central California from Monterey north to Humboldt County. It is frequent in the understory of the closed-cone pine forests at Monterey and may serve as an indication of considerable fog and a rainfall of at least twenty to forty inches.

The genus *Garrya* has been described from Pliocene beds of Bennett Valley and Coalinga, California (Dorf, 1930). In the Pleistocene the only known records are based on specimens closely referable to the modern *G. elliptica*. The Pleistocene specimens from Carpinteria, and Santa Cruz Island are both south of the present range.

EQUISETUM cf. HIEMALE var. CALIFORNICUM Milde (fig. 4, a). Portions of stem occur throughout the beds from Terrace 1 and are particularly abundant in the exposure along the roadcut. They are preserved as internal casts, showing only the nodes and no sheaths; the stems average 8–10 mm. in diameter. The internodal ridges are well preserved; the average number is approximately 30.

The specimens could be referable either to *Equisetum laevigatum* or *E. hiemale* var. *californicum* as far as diameter (2–8 mm. or 5–15 mm. respectively) is concerned. However, the fossils are larger and more



FIG. 4. Fossils from Little Sur travertine deposits. *a*, *Equisetum* cf. *hiemale* var. *californicum* Milde. Portion of stem.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-9. *b*, *Ceanothus* cf. *griseus* (Trel.) McMinn. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-10. *c*, *Ceanothus* cf. *griseus* (Trel.) McMinn. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-11. *d*, *Garrya elliptica* Dougl. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-12. *e*, *Quercus agrifolia* Nee. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-14. *f*, *Garrya elliptica* Dougl. Portion of leaf.  $\times 1$ . Univ. Illinois Paleobot. Coll., Hypotype L-13.

robust in general than *E. laevigatum*. The two distinct rows of silica tubercles also tend to indicate *E. hiemale* var. *californicum*.

Potbury (1932) reported small portions of *Equisetum* stems with nodes and portions of internodes from the San Bruno deposits. There was no previous report of *Equisetum* in the California Pleistocene but Potbury predicted that it would be recorded.

*Equisetum hiemale* var. *californicum* is found living alongside streams and in marshy places from southern California to Humboldt County and thence north to Alaska.

CAREX spp. and JUNCUS spp. Abundant sedge-like leaves and stems occur throughout the beds of the various terraces. There are the usual signs of curling or inrolling of the leaves. They vary in width from 2 mm. to 18 mm., the most common range being 2.5–5 mm. They give the general appearance of leaves of sedges with very prominent vertical stria-

tions. A few flat leaves approximately 15–18 mm. wide might indicate *Typha latifolia*; however, lack of horizontal striations makes this identification seem unlikely. The stems are circular and hence would not be sedges which have a triangular cross section. Along the streams and springs in the area at present both sedges and rushes are common. Grasses, however, can not be excluded as a possibility, but sedges seem more probable in a hot springs environment. Along the edge of Terrace 2 masses of sedge appeared to be in growth position, bent in such a manner as to indicate water flowing downhill. On this terrace almost any portion of travertine sampled for fossils produced masses of these *Carex* and/or *Juncus* leaves.

*Carex* is known from both the San Bruno and Tomales Pleistocene deposits in California. In both cases, perigynia, which are a much better means of identification than leaves, were preserved. There is no record of *Juncus* from the California Pleistocene, but there is no reason why it should not be expected.

ALGAE. In several beds tangled masses of fibrous filaments occur which give the appearance of algae. A sample was tested for the presence of spores but no recognizable forms were recovered. Thus determination of these obvious algal remains can not be made.

Certainly the presence of algae is to be expected in travertine deposits. Davis (1897) states that algae are responsible for the peculiarities in structure of travertine, i.e. the formation of filaments, ropes, beads, tufts, etc. Otherwise he believes that the calcium carbonate would be laid down "like coats of whitewash." The algal inhabitants of hot springs are all members of one or two families, closely related to one another, as conditions are generally not suitable for most algae. Emig (1917) states that in the Arbuckle Mountains of Oklahoma there is a natural cycle of plants that accompanies the appearance and development of travertine. During the earliest states of development the unicellular green algae (i.e. *Protococcus*) and blue-green algae (i.e. *Oscillatoria* and *Lyngbya*) are present, followed by filamentous green algae (i.e. *Vaucheria*, *Oedogonium*, *Rivularia*, *Cladophora*, et al.) that grow in felt-like masses. Also mosses that aggregate in dense tufts are present.

#### VEGETATIONAL RELATIONSHIPS

An assemblage of the recognized plants in the fossil assemblage indicates a closed-cone pine forest with streams or springs along or through the forest. The forest apparently included *Pinus radiata*, possibly *P. muricata*, and *Cupressus goveniana*. There is likewise a possibility of *Pseudotsuga menziesii*. The understory trees include an abundance of *Garrya elliptica*, *Ceanothus griseus*, lesser amounts of *Quercus agrifolia* and possibly *Myrica californica*. Understory shrubs include *Rubus parviflorus*, *Rubus vitifolius* and *Ribes sanguineum*. Springs are necessary to the formation of travertine, and thus the presence of *Equisetum* as well as sedges, rushes, and algae was to be anticipated.

It appears probable that in this area there was a closed-cone pine forest along a canyon or swale with travertine being deposited along a stream-hot spring area. Perhaps as the hot springs became more active, immediately adjacent trees and shrubs were killed, possibly accounting for the abundance of needles of *Cupressus* and leaves of *Ceanothus* and *Garrya*. Likewise as activity became even more extensive, only sedges and rushes could persist, hence their prevalence in certain portions of the terraces.

The present vegetation surrounding the area of the terraces gives no evidence of closed-cone pine forest. It is predominantly a coastal sage pattern, which generally is characteristic of the drier and rockier slopes of the outer California Coast Ranges. The major dominant in the Little Sur area is *Artemisia californica* with *Baccharis pilularis* very abundant. *Salvia mellifera*, *Rhus diversiloba*, and *Pteridium aquilinum* also are common. *Eriogonum* spp., *Eriodictyon crassifolium*, *Diplacus aurantiacus*, *Dendromecon rigida*, *Agastache* spp. are scattered although locally common.

Temporary streams occupy most of the nearby ravines and gullies, although a few apparently have a year-round source of water. An occasional wind-trained redwood and *Photinia arbutifolia* occur in such sites. About a quarter of a mile south of the terraces there is a semi-permanent stream with *Salix scouleriana*, *Amelanchier alnifolia*, *Cornus californica* and *Rhamnus* spp. forming a dense shrubby overstory. The understory consists of *Equisetum telmateia* and *Stachys chamissonis*, with *Rubus vitifolius* climbing over the other plants. Species of *Carex* and *Juncus* are also present.

Coastal sage is the predominant vegetation pattern northward from the terraces to approximately Bixby Creek (about 3 miles from Little Sur River) where species of *Ceanothus* and *Arctostaphylos* form a dense chaparral cover. From thence north to Carmel, coastal sage and chaparral alternate, with the latter occupying the more mesic sites such as north-facing slopes. *Pinus radiata* and *Cupressus goveniana* do not appear until near Carmel. The forest occupying the ridge between Carmel Bay and Monterey Bay is probably the best developed closed-cone pine forest in central and southern California. This forest occupies the entire Monterey Peninsula to the exclusion of other forest types, but extends only a few miles into the interior, and only a short distance to the north as well as to the south. Whether this forest was more extensive in the early history of white man is not known, but there is record of lumbering operations. Also pine roots have been found in the soil to the north and Mason (1934) states that it is probable on the basis of typically associated species that the forest once extended northeastward to the Salinas River.

To the immediate south of the area, coastal sage is replaced by grassland with scattered oaks (primarily *Quercus agrifolia*), thence into a local redwood forest in the Big Sur area. Southward the only known groves of *Pinus radiata* occur near San Simeon and Cambria. The forests are similar in aspect to those of the Monterey region but not as rich in species.

Occasional individuals of *P. muricata* and the kinds of shrubs suggest more favorable soil conditions than at Monterey. In the Pecho Hills, pine is largely replaced by a dense live oak assemblage. Neither pines nor *Ceanothus* occur in an assemblage at Purisima Ridge that is otherwise like the Monterey forest. *Pinus radiata* var. *binata* likewise occurs on Guadalupe Island.

Despite the fact that obviously only a small portion of the forest flora was preserved in the travertine, the pattern of the flora fits that of the modern Monterey closed-cone pine forest. The entire forest there is dominated by *Pinus radiata*; the most conspicuous understory tree is *Quercus agrifolia* with scattered trees of *Myrica californica* and *Umbellularia californica*. The most characteristic feature of the forest is the extensive chaparral-like ground cover made up of species of *Ceanothus* and *Arctostaphylos* associated with a number of other shrubs such as *Adenostoma*, *Lonicera*, *Ribes*, *Rosa*, *Rubus*, *Symphoricarpos*, et al. At slightly higher elevations *Cupressus goveniana* occurs, whereas *Pinus muricata* is found in areas of greatest summer fog and heaviest winter rainfall. Mason (1934) points out that local variations in ecological aspect of the forest flora seem to be related to depth and character of the soil as well as atmospheric moisture. Thin, rock soil layers contain dense brush and in some cases take on an aspect of typical pine barrens. The largest trees and most open forest occur when soil is deep and ground water abundant. From the possible presence of *P. muricata* as well as *Cupressus*, it appears that the forest at the time of travertine deposition might have been at a site with considerable fog. *Myrica* likewise indicates this. The preponderance of *Garrya elliptica* and relatively few preserved specimens of *Quercus agrifolia* are noteworthy. It is likewise interesting that there is an abundance of *Ceanothus* but no record of *Arctostaphylos*, which one would expect to be preserved more easily than the *Ceanothus*. The abundance of *Ribes* and *Rubus* are to be expected in a more mesic aspect of the forest such as one finds along streams or shaded canyons, and probably on deeper soils.

#### VEGETATIONAL HISTORY

The present distribution of the closed-cone pine forest is highly discontinuous (fig. 2). The northernmost outpost is Trinidad Head in northern California, where it is almost obscured by redwood forest. There then is a gap 100 miles south to Inglenook where it occurs as typical coastal forest for about 100 miles to Fort Ross. After a 50-mile break it recurs on Inverness Ridge across from the fossil localities at Tomales Bay. Some remnants also occur on San Gerónimo Ridge in Marin County. There is another 75 mile gap to Point Año Nuevo where another small grove occurs, then another 40 miles to the south end of Monterey and Carmel bays where there is an extensive forest. It is another 60 miles south to San Simeon and Cambria before the forest type is encountered again, and thence southward to the isolated patches occurring at Pecho Hill's and



La Purísima Ridge. There is another break on the mainland of 500 miles to Point San Quintín, Baja California, Mexico. Remnants of closed-cone pine forests also occur on Cedros Island 150 miles south of Point San Quintín, and on Guadalupe Island 200 miles off the coast of Baja California. They also occur on Santa Rosa and Santa Cruz islands of the Channel group.

These modern forests are not homogeneous floristically or ecologically. Evidence from fossil deposits from such widely separated areas as Tomales Bay, Carpinteria and Santa Cruz Island indicates that this forest assemblage is a relict of a past flora and that it was more homogeneous throughout its range in the past than today (Mason, 1934). Mason also points out that the present discontinuity is due to significant geological events, and that for a relatively long interval of time the forest type occupied an extensive area, of which its modern occurrences are but fragments. In all localities in the Pliocene and Pleistocene where fossil records of closed-cone pines are known, the site of deposition has been along one of the major fault lines in the California Coast Ranges. Likewise in all cases the areas occur along fault zones near a block that has been positive throughout the Pliocene at least. Most conspicuous are the blocks severed from the mainland by the San Andreas fault. In the Pleistocene deposits some of the plant materials have come from lands uplifted since the Pliocene but presence of sediments from older landmasses has always been demonstrable.

Mason likewise states that the closed-cone forests today are confined to lands that were islands throughout much of the Tertiary and particularly during the Pliocene. Homogeneity of species content and absence of other contemporary assemblages in the Pleistocene support this hypothesis. This insular relationship is further supported by the high degree of endemism among the forest species: 58 per cent of the woody plants are endemic to the California floristic province with 29 per cent of the above restricted to closed-cone pine forests. This is remarkable considering the very small area of the California province occupied by closed-cone pines. Because most of the endemic species have closely related species elsewhere in the Coast Ranges, it appears probable that there was insular isolation with water barriers. Also the relation of the modern flora to that of the islands off of southern California is important. Several species such as *Vaccinium ovatum* and *Arbutus menziesii* have their southward extension on islands or occur on the southern mainland only in localities that appear to have been Tertiary islands. *Pinus radiata* grows in the general region of Monterey Bay, Morro Bay and on Guadalupe Island (200 miles off the coast of Baja California), but does not grow on the mainland in between. The sporadic occurrence of *Cupressus* from Guadalupe Island to coastal Mendocino County also is another similar distribution. *Cupressus* is known to have occurred in every closed cone-pine forest of which there is fossil record. In many areas it now is extinct, e.g. Santa Barbara region and Santa Cruz Island. Likewise *Pinus radiata* has disappeared

from both of these localities, and both *P. radiata* and *Cupressus* are now absent from Tomales Bay although they were common there during the Pleistocene.

Mason further indicates that the major differences in aspect that prevail in the forest throughout its range today are due primarily to the mingling of the original species with those of migrating populations and consequent selection of floras due to changing climatic conditions in Pleistocene and Recent time. The California insular floras are considered by Mason to represent the original vegetation of coastal California prior to their invasion by continental floras. The discontinuous closed-cone pine forests along the California coast are the last remnants of these insular floras. The fossil occurrences described in this investigation give additional documentation of the former more extensive distribution of this vegetation type.

#### SUMMARY

An assemblage of plant fossils from travertine terraces in Monterey County, California, provides additional documentation of a former more extensive distribution of closed-cone pine forests during the Quaternary. The travertine terraces are considered to be 10,000 or more years old as evidenced by amino-acid dating of gastropod shells in the travertine and substantiated by the topographic relationships of the deposits. The plant fossils are relatively poorly preserved impressions of leaves, with a few casts of stems and cones. Despite the fragmentary record, the forest apparently included *Pinus radiata*, *Cupressus goveniana* and possibly *Pinus muricata* and *Pseudotsuga menziesii*. An abundance of *Garrya elliptica*, *Ceanothus griseus*, lesser amounts of *Quercus agrifolia* and possibly *Myrica californica* occurred as understory trees. *Rubus parviflorus*, *Rubus vitifolius* and *Ribes sanguineum* var. *glutinosum* comprise the recorded understory trees. *Equisetum hiemale* var. *californicum* as well as sedges, rushes and algae also occurred commonly. Thus it appears probable that there was a closed-cone pine forest along a canyon or swale with travertine being deposited along a stream—hot spring area. The present vegetation surrounding the area of the terraces, being predominantly a coastal sage pattern, gives little evidence of closed-cone pine forest. The pattern of the fossil flora, however, fits closely that of the modern closed-cone pine forest on the Monterey peninsula. The location of the travertine terraces also generally supports Mason's (1934) conclusion that fossil records of closed-cone pines have occurred near fault blocks that were positive during the Pliocene. This insular relationship helps to account for the highly discontinuous and endemic nature of the floras.

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## LITERATURE CITED

- AGARDH, C. 1827. Aufzählung einiger in den österreichischen Ländern gefundenen neuen Gattungen und Arten von Algen, nebst ihrer Diagnostik und beigefügten Bemerkungen. *Flora* 10:625-640.
- CHANEY, R. W. and H. L. MASON. 1930. A Pleistocene flora from Santa Cruz Island, California. *Carnegie Inst. Publ.* 415:1-24.
- . 1933. A Pleistocene flora from the asphalt deposits of Carpinteria, California. *Carnegie Inst. Publ.* 415:45-79.
- COHN, F. 1862. Einen Vortrag über die Algen des Karlsbader Sprudels und deren Antheil an der Bildung des Sprudelsinters. *Flora* 45:538-540.
- DAVIS, B. M. 1897. The vegetation of the hot springs of Yellowstone Park. *Science*, NS 6:145-157.
- DORF, E. 1930. Pliocene floras of California. *Carnegie Inst. Publ.* 412:1-108.
- EMIG, W. H. 1917. Travertine deposits of Oklahoma. *Okla. Geol. Surv. Bull.* 29:1-76.
- FROST, F. H. 1927. The Pleistocene flora of Rancho La Brea. *Univ. Calif. Publ. Bot.* 14:73-98.
- GLEN, WILLIAM. 1959. Pliocene and lower Pleistocene of the western part of the San Francisco peninsula. *Univ. Calif. Publ. Geol. Sci.* 36(2):147-198.
- JEPSON, W. L. 1925. A manual of flowering plants of California. Univ. Calif. Press. Berkeley.
- JONES, J. C. 1914. The tufa deposits of the Salton Sink. *Carnegie Inst. Publ.* 193:79-84.
- KELLERMAN, K. F. and N. R. SMITH. 1914. Bacterial precipitation of calcium carbonate. *Jour. Wash. Acad.* 4:400-402.
- MASON, H. L. 1927. Fossil records of some west American conifers. *Carnegie Inst. Publ.* 346:139-158.
- . 1934. Pleistocene flora of the Tomales formation. *Carnegie Inst. Publ.* 415:81-179.
- . 1940. A Pleistocene record of *Pseudotsuga macrocarpa* [Carpinteria, California]. *Madroño* 5:233-235.
- . 1942. Distributional history and fossil record of *Ceanothus*, in *Ceanothus* by M. van Rensselaer and H. E. McMinn. Santa Barbara Bot. Gard.
- . 1957. A Flora of the Marshes of California. Univ. Calif. Press. Berkeley and Los Angeles.
- McMINN, H. E. 1942. A systematic study of the genus *Ceanothus*, in *Ceanothus* by M. van Rensselaer and H. E. McMinn. Santa Barbara Bot. Gard.
- MEUNIER, S. 1899. Observations relativ du depot de certain travertins calcares. *Compt. Rend. Acad. Paris* 129:659-666.
- MUNZ, P. A. and D. D. KECK. 1959. A California flora. Univ. Calif. Press. Berkeley and Los Angeles.
- POTBURY, SUSAN S. 1932. A Pleistocene flora from San Bruno, San Mateo County, California. *Carnegie Inst. Publ.* 415:25-44.
- SIMMONDS, R. T. 1962. Wisconsin Geochronological determinations based upon amine decay rates. Ph.D. dissertation, Dept. Geol., Univ. Illinois, Urbana.
- TRASK, P. 1926. Geology of Point Sur Quadrangle, California. *Univ. Calif. Publ., Bull. Dept. Geol. Sci.* 16:119-186. Pl. 16.
- TWENHOFEL, W. H. 1950. Principles of sedimentation. McGraw-Hill. New York.
- WEED, W. H. 1888. Formation of travertine and siliceous sinter by the vegetation of hot springs. *U.S. Geol. Surv. Ann. Rept.* 9:613-676.